

ON REFLEX ACTION FROM SYMPATHETIC GANGLIA.

BY J. N. LANGLEY, F.R.S., *Fellow of Trinity College*, AND
H. K. ANDERSON, M.B., *Caius College, Cambridge*.

Two cases only, of reflex action occurring in peripheral ganglia, have been brought forward with sufficient evidence to demand careful consideration. These are—(1) the reflex from the sub-maxillary ganglion of the dog, described by Claude Bernard¹, and (2) the reflex from the inferior mesenteric ganglion of the cat, described by Sokownin². In the former case the action thus produced is the secretion of saliva from the sub-maxillary gland, in the latter case it is a contraction of the bladder.

REFLEX ACTION OF THE SUB-MAXILLARY GANGLION ON SECRETION.

With regard to the secretion of saliva in the given circumstances, the great majority of physiologists adopted till recently the explanation given by Schiff³, viz. that it is due to the stimulation of recurrent fibres of the chorda tympani. And it would have been unnecessary to give any further attention to this matter but for a paper published by Wertheimer⁴, in which he reasserts that the true explanation of the facts is the occurrence of a reflex in the peripheral ganglia on the course of the chorda tympani.

Wertheimer arrives at this conclusion, since, repeating one of the experiments relied on by Schiff, he obtains a diametrically opposite result. The lingual nerve is cut two to four centimetres below the

¹ Claude Bernard. *Journ. de Physiol.* 1862, p. 400. It may be recalled that the 'sub-maxillary ganglion' of Bernard is in the main a sub-lingual ganglion; and that the true sub-maxillary ganglion lies in the hilus of the gland (cp. Langley, *This Journal*, xi. 123. 1890).

² Kowalesky and Arnstein. *Pfûger's Archiv*, Bd. viii. p. 600. 1874.

³ Schiff. *Leçons sur la Physiol. de la Digestion*, i. 284. 1867. For an account of the controversy on the subject see Foster's *Text-Book of Physiology*, Ed. iii. p. 240. 1879.

⁴ Wertheimer. *Arch. de Physiol. norm. et path.* 1890, p. 519.

point where the chorda tympani and lingual nerves diverge, and the animal is left for six or seven days so that the cut recurrent fibres may degenerate. Then the chordo-lingual nerve is severed centrally of the 'sub-maxillary' ganglion, and the portion of the lingual central to the first cut, i.e. the part supposedly attached to the ganglion, is stimulated. The stimulation according to Schiff has no effect; Wertheimer finds that it produces a flow of saliva.

Both Wertheimer and Schiff state that in such an experiment all the recurrent fibres have been cut and have degenerated. Naturally Wertheimer contests Schiff's deduction; he argues that as the secretion which he obtains cannot be due to recurrent fibres, it must be due to the stimulation of afferent fibres which run from the tongue to the sub-maxillary ganglion, stimulation of these causing a reflex action in the ganglion.

It is obvious, however, that the major premiss of this argument is unsound; the section of the lingual will only cause degeneration of those recurrent fibres which curve back below the point of section; those fibres which take their recurrent course centrally of the point of section will remain normal, just as the chorda tympani remains normal; and stimulation of these will produce a secretion, just as does stimulation of the chorda tympani.

Of the existence, in some cases, of nerve-fibres which accompany the lingual and then turn back towards the salivary gland there can be no doubt. Wertheimer himself describes one such case. We have traced anatomically such fibres leaving the lingual nerve at varying distances, up to three and a-half centimetres from the region where the chorda tympani leaves the lingual. Such fibres usually join the chorda tympani after it has run a centimetre or more on its course¹.

In the absence of accurate knowledge of the number and course of the recurrent fibres in each individual case, it may be said with certainty that experiments like those of Wertheimer do not, and cannot, prove that the sub-maxillary ganglion has a reflex function.

The controversy, then, stands much as it has stood for many years past, and it is hardly necessary to give the other known facts on either side. On reviewing them, it seemed to us that the sub-maxillary ganglion was an unfavourable one for the study of the main question, and we turned to the other asserted instance of a reflex, for whatever general statements can be made of any one sympathetic ganglion may

¹ On the other hand, it must not be overlooked that in all probability many of these fibres run to the sub-lingual and not to the sub-maxillary gland.

with a high degree of probability be applied to all other ganglia belonging to the sympathetic type.

REFLEX ACTION OF THE INFERIOR MESENTERIC GANGLION
ON THE BLADDER.

The earliest mention which we find of this action is in 1874 in an abstract of a paper of Sokownin's¹; it is simply stated that the sensory fibres which run to the bladder by way of the hypogastric nerves have their reflex centre in the inferior mesenteric ganglion. A fuller statement was published in Russian in 1877. In the summary² of this, the work is said to have been done under the direction of Kowalesky. In a curarised cat, all the branches of the inferior mesenteric ganglion were cut, except the two hypogastric nerves. One hypogastric was cut and its central end stimulated, this gave contraction of the bladder; similar stimulation was without effect after the opposite hypogastric had been tied immediately below the ganglion. The afferent portion of the reflex chain was supposed to consist of sensory fibres running from the bladder to the ganglion.

The experiment was repeated and confirmed by H. Nussbaum³. More recently it has been again repeated and confirmed by Navrocki and Scabitschewsky⁴, who add that the reflex can also be obtained by pinching the central end of the hypogastric nerve, i.e. by mechanical stimulation. Lastly it has been confirmed by ourselves⁵.

Nomenclature of branches of the inferior mesenteric ganglion. A general description of the inferior mesenteric ganglion in the cat has been given by Sokownin⁶ and by Navrocki and Scabitschewsky⁷. Speaking broadly, it may be said to consist of two ganglia on each side, one just above, and the other just below, the inferior mesenteric artery, the ganglia being connected by nerve-strands; this, however, represents its complexity but imperfectly. The ganglia and the nerves connected with them are in the main bilaterally symmetrical. The nerves, usually three, which, on each side, run from the spinal cord, traversing the sympathetic trunk, are called by Navrocki and Scabit-

¹ Sokownin. *Pfűger's Archiv*, Bd. viii. p. 600. 1874.

² Sokownin. *Hofmann and Schwalbe's Jahresb.* 1877, Bd. 6, ii. p. 87.

³ H. Nussbaum. *Hofmann and Schwalbe's Jahresb.* 1879, Bd. 8, ii. p. 64.

⁴ Navrocki u. Scabitschewsky. *Pfűger's Archiv*, Bd. 49, p. 141. 1891.

⁵ Langley and Anderson. *Proc. Physiol. Soc. May*, 1893 (*This Journal*, xv.).

⁶ *loc. cit.* 1877.

⁷ *Pfűger's Archiv*, Bd. 48, p. 335. 1891.

schewsky, mesenteric nerves; they correspond with the splanchnics, and they might more appropriately be called the inferior or lower splanchnics; we shall generally speak of them as the spinal branches to the ganglia. From each side, nerves are given off towards the colon, forming as they go a plexus around the peripheral part of the inferior mesenteric artery; these we shall call the colonic nerves. From the upper end of the upper ganglia, two or more strands run close together towards the solar plexus; as these consist in part of fibres running from the ganglia, they may be called the ascending branches; not infrequently, however, a spinal branch on each side joins the ascending branches and runs alongside them to the ganglion. Commonly each hypogastric nerve about three-quarters of an inch from the ganglion gives off a small strand—an accessory hypogastric—which runs in the more dorsal part of the mesentery towards the pelvic (hypogastric) plexus. The right hypogastric appears to be, as a rule, larger than the left.

In nearly all our earlier observations we took tracings of the internal pressure of the bladder, showing the occurrence of contraction or dilation of its walls. A German silver catheter pierced with holes in its terminal inch was passed through the urethra into the bladder, and the urethra tied round it. This was connected with a T tube, one end of which was connected with a vessel having several openings, one for a thermometer, one to allow fluid to run out, another connected with a burette by which fluid could be allowed to run in, and a fourth connected with a vertical glass tube. The vessel was filled with .75 p.c. salt solution, and was kept at any required temperature by means of a spirit lamp underneath it. The vertical glass tube was 4.5 centimetres in diameter, and on the salt solution in it was a glass bulb serving as a float; to the upper end of the float was attached a thread which passed over a wheel, and so down to a counterpoised marker, the end of which wrote upon a slowly revolving drum, the marker being arranged so that a contraction of the bladder caused a rise in the tracing. The whole was placed on a screw stand, so that the marker could be moved towards or away from the drum. The vessel could be raised or lowered by means of a screw, and the wheel carrying the thread to the lever could also be raised or lowered by an independent screw; further, the animal could be raised or lowered. The tracings were taken sometimes with the ventral, sometimes with the dorsal surface of the animal uppermost (cp. p. 422); in the latter case, the abdominal wall was cut through along the edge of the quadratus lumborum, and the nerves dissected from the side.

Altogether the apparatus was rather complicated, but it is hardly necessary to describe it in further detail as everyone will probably use his own methods of obtaining the desired ends, viz. of varying the pressure in the bladder, of keeping the fluid in the bladder at about 38° C., and of conveniently obtaining a tracing of the pressure in the bladder, and so noting its contractions and dilations.

The chief trouble which besets this form of experiment is the frequent occurrence of spontaneous and irregular contractions. These are generally the more marked the more the bladder has been exposed and handled. In part they appear to be due to reflexes through the sacral nerves, caused by stimuli passing to the spinal cord from the viscera which have been exposed; and thus, as mentioned by Sherrington, they can often be much reduced, and sometimes even abolished, by giving chloroform and ether in considerable excess; the diminution of the contractions caused by anæsthetics is accompanied by a considerable loss of tone. The cooling of the fluid in the bladder may increase the rhythmic contractions; and in consequence they may sometimes be diminished by emptying the bladder and refilling it with .75 p.c. salt solution at 38° C. Lastly, stimulation of the motor nerves to the bladder is favourable to the production of a rhythm. In a few only of our experiments was the bladder quiescent, though in one case there was no contraction, except on stimulation, during four hours. As a rule there was rhythmic contraction more or less pronounced; in these cases we usually stimulated the hypogastric or other nerve just after the marker began to fall, i.e. at the beginning of the dilation of the bladder.

We have made 18 experiments on the cat, taking a tracing of the internal pressure of the bladder (Series A). The general method of these experiments was as follows:—

The anæsthetics used were chloroform, followed by the A.C.E. mixture, and sometimes in addition 1 to 2 c.c. of 2 p.c. morphia acetate was injected into a vein. One hypogastric nerve—sometimes the right, sometimes the left—was tied an inch to an inch and a quarter from the inferior mesenteric ganglion, and cut peripherally of the ligature. The mesentery was cut through for about three-quarters of an inch on each side of the inferior mesenteric artery, close to its origin, and the mesentery, with any nerve filaments, torn away from this region of the artery. From the upper cut in the mesentery, another cut was made towards the colon, so as to sever any nerve which might run to the ganglia in the upper portion of the mesentery. Thus all the connections

between the ganglia and the sympathetic chain and so the spinal cord were severed. Sometimes the branches proceeding from the ganglion to the intestine by the inferior mesenteric artery were also severed.

The pubic symphysis was cut through, the catheter passed through the urethra into the bladder, and the urethra tied round the catheter.

In some cases a portion of the spinal cord was also removed, the smallest portion removed being from the sixth lumbar segment downwards, the largest portion being from the xth thoracic segment downwards.

A tracing of the pressure inside the bladder was then taken. The central end of the cut hypogastric nerve was stimulated, and the effect on the tracing noted. Commonly, three strengths of stimuli were used: first, one such that the shocks could not be felt on the tip of the tongue, then one such that the shocks were felt feebly on the tip of the tongue, and lastly, one such that the shocks were felt rather strongly. In some cases the central end of the hypogastric was pinched several times with a fine pointed forceps, and the effect on the tracing noticed.

Then the opposite hypogastric nerve was cut, and the first used hypogastric again stimulated. Lastly, the effect of stimulating the *peripheral* end of the opposite hypogastric was observed.

In this way we obtained incontestable proof that after cutting all the nerves connected with the inferior mesenteric ganglion except the hypogastrics, stimulation of the central end of one hypogastric nerve by tetanizing shocks or by pinching, still causes contraction of the bladder.

We do not, however, think the method given above is a favourable one for demonstrating the effect.

Stimulation of the peripheral end of one hypogastric, unlike that of the *nervus erigens*, causes a brief contraction only, which squeezes 3 to 8 c.c. of fluid from the bladder. The stimulus must not be repeated at too short intervals, or the effect will be reduced and may temporarily disappear. The contractions produced are not unlike the spontaneous contractions, and consequently when the latter are large and of an irregular character, it may be impossible except after repeated trials to be certain that the contraction which follows the stimulation is really produced by it. But on repeated stimulation, the effect is apt to be much diminished. And thus we have sometimes found, especially towards the end of an experiment, that the *peripheral* hypogastric fails to give prompt and satisfactory proof of its influence. These stumbling-blocks in the way are much more serious in observing the effect of

stimulating the *central* end of the hypogastric, for the contractions produced by it are weaker and fatigue sets in sooner. In favourable circumstances stimulation of the central end of the nerve causes ejection of about 3 c.c. of fluid from the bladder, the form of the curve obtained on the tracing being the same as that obtained when the peripheral end is stimulated.

We have said above that we have made 18 experiments by the graphic method. In 7 the central end of the hypogastric gave repeatedly distinct contraction; in 8 it gave sometimes a distinct contraction, sometimes a doubtful effect, sometimes none; in 3 it gave no certain effect. In two of the 3 experiments last mentioned the peripheral end of the opposite hypogastric had also a very feeble effect.

In all our later experiments we have reverted to the method of direct observation of the bladder, and for several reasons. The pressure of fluid in the bladder, and even the presence of dilute salt solution, seems to us to increase the spontaneous contractions; occasionally, on stimulating the hypogastric there is a fall of the lever, as if there were a dilation of the bladder; the graphic method is much more troublesome than that of direct observation; and direct observation gives, we think, more constant results.

It is true, generally speaking, that when an organ contracts of itself there is very considerable risk, in the absence of a graphic record, of mistaking a contraction that simply follows a stimulus for one produced by it. This risk is however less, the more marked the effect of the stimulus. In the bladder the spontaneous contractions have, to the eye, a different character from those produced by stimulation of one hypogastric. The spontaneous contraction, though by no means simultaneously involving all parts, commonly does involve all parts. The contraction produced by the hypogastric nerve is strongest in the neighbourhood of the opening of the ureter, and in the main is confined to one side of the bladder.

Distension of the bladder seems to us to be detrimental to the distinctness of the contraction, hence we nearly empty it at the beginning of an experiment. The effect of stimulation is obvious when the bladder is apparently quite empty and tightly contracted.

During the dissection the viscera are covered up with pieces of warm flannel, several of which are kept in salt solution at 40° C. and wrung out as required. A minute or more before stimulating the nerve, the bladder is turned towards the pelvis so that its dorsal surface can be observed.

We have made numerous experiments (Series B) in which the bladder was observed directly, but otherwise following the method described above (p. 414), and with most satisfactory results. The chief precaution to take is to refrain from stimulating the central end of the hypogastric at too short intervals. There is some difference in the extent of the contraction in different individuals; and so far as our observations go, the less marked the contraction, the less marked are the strands connecting the ganglia of the two sides.

The isolation of the inferior mesenteric ganglion can be simplified and made absolutely certain, by proceeding in the following way. One hypogastric is ligatured and cut, the central end is held up by the ligature, and the mesentery on either side of it cut through up to the ganglion; pulling gently on the ligature, the ganglia above the artery are cut away and all the branches of the lower pair of ganglia, except the opposite hypogastric, the mesentery on either side of this is cut through; thus, the central end of one hypogastric, the lower pair of ganglia, and an inch or more of the opposite hypogastric can be held up in the air. A stimulus started in the cut hypogastric can only reach the body by passing through the ganglia and the opposite hypogastric. On stimulating the central end of the cut hypogastric, obvious contraction of the bladder follows.

OTHER REFLEXES FROM THE INFERIOR MESENTERIC GANGLION.

When we had obtained sufficient proof of the truth of the previous accounts as to the occurrence of a reflex action on the bladder, we turned our attention to the question of the occurrence of other reflexes of a similar nature. Contraction of the bladder is but one of a number of actions under the control of the hypogastric nerves. The other obvious and constant effects produced by them in the cat are, contraction of the internal sphincter of the anus¹ with pallor of the mucous membrane of the end of the rectum, and unilateral pallor of the uterus (or vas deferens and prostate vesicle). An effect which varies widely in distinctness in different individuals is contraction of the uterus (or vas deferens and prostate vesicle); besides this there may be slight contraction and pallor of the vagina (or penis); pallor and contraction of the

¹ This contraction might be regarded as a contraction of the rectum, but as it is at its maximum close to the anus and diminishes upwards, not being visible so far as we have seen in the upper part of the rectum, we think it more accurate to call the contracting muscle, the internal sphincter of the anus.

end of the colon and the rectum, and apparently sometimes paling of the bladder. The contraction of the internal sphincter if strong is visible externally, and may be accompanied either by an anterior or a posterior movement of the anus; it is however best seen by dragging open the external sphincter; the pallor of the uterus is often slow, though finally very complete.

The preliminary preparation for isolating the inferior mesenteric ganglion is of course the same as that already given, and need not be repeated.

We find that stimulation of the central end of one hypogastric after isolation of the inferior mesenteric ganglion gives marked contraction of the internal sphincter of the anus, and pallor of the mucous membrane of the end of the rectum. If intervals of a minute or two are allowed between successive short stimuli, the effect is obtained constantly and apparently for as often as one chooses to repeat the stimulus. The quickness and strength of the contraction vary in different individuals; it may be more, or it may be less, striking than the contraction of the bladder. The spontaneous rhythmic contractions which sometimes occur interfere with the observation only when the contractions for any reason (e.g. insufficient strength of stimulus or interference with the blood supply) are feeble. Occasionally there is a little difficulty with the external sphincter of the anus. For this, if the sacral spinal cord is intact, may have at times strong rhythmic movement.

If the colonic nerves are left in connection with the ganglion, then, sometimes, section of one hypogastric weakens but does not annul the internal sphincter effect of stimulating the central end of the other hypogastric. Apparently, impulses travelling up the hypogastrics, may pass to the internal sphincter by the colonic nerves. Further, we have seen a weak contraction of the internal sphincter on stimulating the central end of a bundle of the colonic nerves. But these are points to which we have not given a great deal of attention.

On the uterus, the central end of the hypogastric has very little effect; not infrequently we have seen slight pallor of the cornu and of the body of the uterus on the opposite side, but once only have we been able to satisfy ourselves that there was a contraction of the musculature of the organ.

On the vagina, we have occasionally seen a slight reflex effect, but more commonly there was none.

We have not observed any other effect with certainty. Thus, the

reflex effects produced by stimulating the central end of one hypogastric, are roughly in proportion to the distinctness of the effects produced by stimulating its peripheral end; the chief variation being the comparatively slight pallor which the central end of the nerve causes in the uterus.

We ought perhaps to mention specially that the reflexes can be obtained by pinching the end of the nerve as well as by applying tetanising shocks.

In one or two cases we severed close to the bladder the nerves running to it; stimulation of the central end of these nerves gave contraction of the bladder and none of the internal sphincter. The result suggests that the reflex in any one organ is only produced by the nerves which run to it; but to determine this requires further experiments.

We have made half-a-dozen experiments on the dog, but without satisfactory results; the reflexes, even on the bladder, were slight and inconstant. In the rabbit, the two hypogastrics run so close to one another for a large part of their course, that it is difficult to isolate a sufficient length of one without injuring the other; we have obtained effects on the uterus and on the descending colon by stimulating the central end of one hypogastric; the latter effects are more obvious when the central ends of both hypogastrics are stimulated.

The point in this section which we would emphasize is that either hypogastric nerve can produce reflexly a marked contraction of the internal sphincter of the anus, and pallor of the mucous membrane of the end of the rectum.

CONSIDERATION OF THE POSSIBLE EXPLANATIONS OF THE REFLEXES.

We take it to be sufficiently proved that stimulation of the central end of a nerve-strand proceeding from the inferior mesenteric ganglion can give rise to impulses which travel down efferent fibres of another nerve-strand proceeding from the ganglion.

The fact is interesting, but in itself it proves nothing as to the really important questions, whether the peripheral ganglia can or cannot act as reflex centres, and if they can whether the reflex action has the same anatomical basis as the reflex actions of the central nervous system.

There are a number of ways of accounting for the fact. We will consider these as far as possible separately. But first we will give an

account of the action of nicotin upon the reflexes since this gives one sure step towards a conclusion.

Action of nicotin on the hypogastric reflexes.

Nicotin, as we know, acts upon sympathetic nerve-cells—or upon the connections of nerve-fibres with them—so that impulses which normally would pass through the cells, do so no longer.

Now if about 20 milligrams¹ of nicotin are injected into a vein of a cat, stimulation of the central end of the hypogastric no longer has any effect. Hence, the impulses set up on stimulating the central end of the hypogastric nerve, must somewhere on their course traverse nerve-cells. These nerve-cells, for the most part at any rate, are not on the course of the peripheral hypogastric, for as was earlier shown by one of us² nicotin does not abolish the effects of stimulating the peripheral end of the hypogastric. The inferior mesenteric ganglion is the sympathetic cell-station for the great majority of the efferent hypogastric fibres; or, in other words, it is the trophic centre for these fibres.

Hence, in whatever way stimulation of the central end of the hypogastric produces its effects, the nervous impulses which pass down the opposite hypogastric and give rise to the various motor phenomena must previously have passed through nerve-cells in the inferior mesenteric ganglion.

As with other sympathetic ganglia, the duration of the paralysis after nicotin depends upon the dose; with a small dose the paralysis may last 15 to 20 minutes only; its disappearance being shown by the return of function both of the spinal branches to the inferior mesenteric ganglia and of the central end of the hypogastric. We give one protocol to illustrate the experiments of this series.

SERIES C.

Action of Nicotin on the Hypogastric Reflexes.

Cat. 1.25. Chloroform, and afterwards A.C.E. mixture. Double tie and cut right hypogastric. The inferior mesenteric ganglion was not isolated, in order to avoid a possible interference with the blood supply to it. Tetanising shocks felt distinctly but weakly on the tip of the tongue.

¹ The minimal dose required appears to be about 10 milligrams, but in order to be on the safe side we have generally given 20 to 50 milligrams.

² Langley. *Proc. Physiol. Soc.* Dec. 1890. (*This Journal*, XII. 1891.)

- 1.47 to 2.15. Stimulation of the central end of the right hypogastric causes contraction of the bladder, chiefly of the opposite side, slow but good contraction of the internal sphincter of the anus, pallor of the mucous membrane of the end of the rectum, a slight, slow paling of the cornu of the uterus of the opposite side; and usually a slight reflex twitch of the muscles of the body. Stimulation of the peripheral end of the right hypogastric causes similar visceral effects to a more marked degree, the effects on the bladder and uterus being chiefly on the same side.
- 2.21 Inject 2 c.c. of 1 p.c. nicotine (= 20 milligrams) into the jugular vein.
- 2.25 Stimulate central end of hypogastric —no effect.
- 2.26 Stimulate peripheral end of hypogastric—effects much as at first.
- 2.27 Stimulate central end of hypogastric —no effect until the electrodes touch the ganglion.
- 2.40 Stimulate central end of hypogastric —no effect.
- 2.50 Stimulate central end of hypogastric —contraction of bladder; ? no effect on internal sphincter.
- Tie and cut spinal branches on the right side.
- 2.53 Stimulate right spinal branches —contraction of bladder; no effect seen on internal sphincter.
- 2.55 Stimulate central end of hypogastric —contraction of bladder; slow contraction and pallor of internal sphincter.
- Cut spinal branches on the left side and the ascending branches, thus isolating ganglion except for the hypogastric and colonic nerves.
- 3.10 Stimulate central end of hypogastric —contraction of bladder, contraction and pallor of internal sphincter.
- Cut away upper part of ganglia, and cut all attachments of the lower pair except the two hypogastrics, thus the right hypogastric is only connected with the body by the peripheral part of the left hypogastric.
- 3.30 Stimulate central end of right hypogastric—slight but distinct contraction of bladder and of internal sphincter.

Having so far limited the possibilities we may proceed to discuss the various alternatives.

Recurrent fibres.

The first view which naturally presents itself is that the explanation given by Schiff and others of the 'reflex' from the sub-maxillary ganglion may serve also for the 'reflexes' under discussion. There is to us nothing unlikely in the view that fibres from the lumbar or sacral nerves might join the hypogastric some considerable distance from the inferior mesenteric ganglion, ascend in it, pass to cells in the

ganglion, and so be connected with fibres which descend in the contralateral nerve. And in fact, two or more branches of the *nervus erigena* are continuous anatomically with the lower end of the hypogastric.

In testing this view we have confined our attention almost entirely to the bladder, since it is in the highest degree unlikely that the meaning of one 'reflex' obtained from the central end of the hypogastric should be different from that of the rest. The usual method employed was to cut on one side close to the bladder all the nerves running to it, and to stimulate the sacral nerves in the spinal canal; or in addition to cut the spinal branches of the inferior mesenteric ganglion, and to stimulate the lumbar nerves in the spinal canal. In such case, if nerve-fibres ascend in the hypogastric, they are uninjured, and stimulation of the spinal nerves giving off these fibres should cause a contraction of the bladder. The state of the bladder was in most cases noted by taking a tracing of the internal pressure (cp. p. 413). The lower part of the animal was suspended in the air by means of clamps attached to the vertebræ, since it was found that in this way the movements of respiration and peristalsis of the intestines had very little effect upon the bladder tracing. Stimulation of the upper lumbar nerves, causing a contraction of the abdominal muscles, naturally gave a rise in the bladder tracing. To avoid this, the nerves were cut just outside the *longissimus dorsi*, or—in one or two cases—*curari* was given as well as anæsthetics. The muscular movements caused by stimulating the lower lumbar and sacral nerves, though violent with some of the nerves, have very little effect on the bladder tracing.

(a) *Sacral Nerves.* We have made six experiments as to recurrent fibres arising from the sacral and adjoining spinal nerves. In these the lower part of the spinal cord was removed and on both sides the sacral and one or more of the adjoining nerves¹ stimulated. Stimulation of the nerves on the side on which the fibres running direct to the bladder were intact served as a control, and showed that the bladder responded readily enough when its motor fibres were stimulated. In four of these experiments there was no suspicion of the presence of recurrent fibres. In the remaining two the irregularity of the rhythmic contractions² made the result less clear, but an inspection of the whole

¹ Up to the sixth lumbar and down to the third coccygeal.

² Cutting the nerve-fibres to the bladder involves more or less interference with the blood supply; sometimes indeed the arteries were ligatured so that the attachments of the bladder on one side could be completely severed. This favours the production of irregular rhythmic contractions.

tracings showed that there was no single case in which contraction could be definitely attributed to the stimulation.

From this it may fairly be concluded that the lower part of the spinal cord sends to the bladder no fibres, which take the indirect route of ascending in one hypogastric to descend in the other.

It must, however, be mentioned that these experiments are open to some criticism. The lower part of the spinal cord sends motor fibres to the bladder by three spinal nerves; so that any one spinal nerve would probably contain not much more than one-third of the nerve-fibres taking the hypogastric route, supposing such nerve-fibres to exist.

Now in the conditions of the experiments, the central end of the hypogastric, i.e. the whole of the assumed nerve-fibres, often gives but a slight and inconstant contraction of the bladder, and hence it might be argued that when a part only of the fibres is stimulated, the contraction would possibly fail altogether. In this set of experiments, the central end of the hypogastric was not stimulated until the spinal nerves had been stimulated repeatedly, so that we could hardly expect the hypogastric to produce its full normal effect. And in fact, it did not do so; in one case only was the contraction marked, in the others it was slight and inconstant.

The criticism may be met by stimulating the *nervus erigens* instead of the sacral nerves, since the latter send their motor fibres to the bladder by way of the *nervus erigens*. We have tried this in three cases by the graphic method, and have not found any effect on the bladder,—the nerves to the organ on the side stimulated being of course cut. We have repeated the experiment, observing directly the bladder and the internal sphincter of the anus and also with negative results.

(b) *Upper lumbar nerves.* If the hypogastric nerve on one side be cut, and on the same side the upper lumbar nerves which send fibres to the bladder be stimulated, we still obtain a contraction of the bladder on the opposite side, contraction of the internal sphincter, and so forth. So, also, if a spinal ramus of the inferior mesenteric ganglion be stimulated, the hypogastric nerve on the same side being cut, there follow contraction of the bladder on the opposite side, and the other effects of stimulating the opposite hypogastric. This means that the upper lumbar nerves of one side of the body send fibres down both hypogastrics. Now the spinal rami to the inferior mesenteric ganglion stretch over a considerable space in the mesentery; these for the most part are anterior to the ganglion, but it might well happen that a few

fibres not obvious as a distinct special ramus should take a more posterior course, curve into the hypogastric and ascend in it to the ganglion. If there were such fibres, we should expect them, like the more obvious spinal rami, to send some fibres down the opposite hypogastric. Here then, as with the sacral nerves, there is some anatomical basis for attributing the 'reflex' to recurrent fibres.

The experiments to test this are on the same lines as those given for the sacral nerves, but are rather more complicated. On one side all the nerves to the bladder are cut through close to it; the obvious spinal rami of the inferior mesenteric ganglion are severed by making a cut through the mesentery, starting about a quarter of an inch below the inferior mesenteric artery and curving anteriorly to it nearly to the colon. Tracings of the internal pressure of the bladder were taken.

In this way four experiments were made, the spinal nerves from the XIIIth thoracic to VIIIth lumbar being stimulated; the stimulation had no effect upon the bladder, i.e. there was no evidence of the presence of recurrent fibres.

Since the upper lumbar nerves sometimes send a few fibres through the lower part of the lumbar sympathetic trunk to the bladder, it seemed possible that these might be recurrent hypogastric fibres. But on cutting both sympathetic trunks just below the VIth lumbar sympathetic ganglia, and leaving six days for degeneration, we still found good reflex contraction of the bladder when the central end of one hypogastric nerve was stimulated.

Hence then we conclude that the various effects which follow stimulation of the central end of the hypogastric nerve are not due to recurrent fibres, i.e. to spinal fibres joining the hypogastric low in its course, ascending in it to the inferior mesenteric ganglion, and proceeding to their terminations in the opposite hypogastric.

Further observations bearing on this point will be given in the subsequent section (p. 425).

We may, then, consider the various effects just spoken of as being due to a reflex action, but the mechanism of the reflex is still to seek.

In the following inquiry into this question, we shall assume, in accordance with the general result of neurological research, that each nerve-fibre has one trophic centre only, and that this trophic centre is a nerve-cell. The primary point, then, to determine is the position of the trophic centre of the nerve-fibres which give rise to the reflexes. The observations made to this end require that certain nerves should be cut

and time given for them to degenerate. The operation was conducted as follows:—the animal, which had not been fed on the morning of the operation, was anaesthetized with ether, the hair in the required region was shaved, the skin washed first with soap, then with 0·2 p.c. HgCl_2 and the nerve or nerves cut; the wound was sewn up with deep and superficial ligatures of carbolyzed chromic catgut. Antiseptic precautions were used; 2 p.c. mercuric chloride, 2·5 p.c. carbolic acid, and boiled 75 p.c. salt solution being employed at their appropriate times. During the stitching of the wound, 1 c.c. of 2 p.c. morphia was injected subcutaneously and the ether discontinued. This served to keep the animal quiet until the collodion dressing had become stiff, and also to prevent the sickness which is apt to occur after ether alone. The animals were left sleeping and the next morning showed no sign of pain, and purred on being stroked; in one case (spinal nerves cut), the animal was drowsy and rather torpid. The diet was milk for a day after the operation, then milk and fish or other food according to the appetite and state of the animal; most of those which underwent abdominal operation had more or less diarrhoea.

Question of trophic centre on the peripheral course of the hypogastric.

If the nerve-fibres subserving the reflexes have their trophic centres on the peripheral course of the hypogastric nerves, these fibres must of course, after section of the hypogastrics, degenerate in the central ends of the nerves. To decide this matter, it is, then, sufficient to cut one hypogastric, and after giving time for the degeneration of the cut fibres, to stimulate the central end with isolated inferior mesenteric ganglion. If the stimulus produces no reflexes, the trophic centre is peripherally of the cut; if, on the other hand, it produces the reflexes as usual, the trophic centre must be centrally of the cut.

We have made five experiments (Series E) in which one hypogastric was cut, and, after an interval, the central end was stimulated. The interval was ten days in No. 1 and No. 2, seven days in No. 3, five days in No. 4 and No. 5.

In No. 1 and No. 2, the reflex on the bladder only was looked for, and this by the graphic method. In one of these, there was a good and constant reflex, in the other, as often happens with this method, it was slight and inconstant.

In the other three, the organs were observed directly; in each of

these, stimulation of the central end of the cut hypogastric gave obvious and indubitable contraction of the bladder; it gave also distinct contraction of the internal sphincter of the anus, though in two of the cases, the contraction was less strong than that which we expect from the normal central end¹.

These positive results show that the nerve-fibres which subserve the reflexes have not their trophic centre on the peripheral course of the hypogastric nerves.

We give some details of two experiments of this series.

SERIES E.

Effect of section of one Hypogastric Nerve.

- No. 3. Cat. Left hypogastric nerve and the largest of the spinal branches on the left side cut 7 days previously. Give chloroform, and then A. C. E. mixture.
- 12.20 Stimulate central end of left hypogastric—good contraction of the bladder and slight contraction of the internal sphincter of the anus, but less strong than usual.
- Tie separately, spinal branches on left side, spinal branches on right side and the ascending branches.
- 1.2 Stimulate central end of left hypogastric—contraction of bladder, slight contraction of internal sphincter of anus.
- Stimulate chief right spinal branch—contraction of bladder, vas deferens and prostate; weakish contraction of internal sphincter.
- Stimulate left spinal branches. —contraction of bladder, vas deferens and prostate; weak contraction of internal sphincter.
- No. 4. Cat. Right hypogastric nerve cut 5 days previously about an inch below the ganglion. Chloroform, then A. C. E. mixture. As abdominal muscles are rather tense, inject morphia and afterwards curari into the jugular. Tie separately the spinal branches on the right and left sides, and the ascending branches.
- Stimulate left spinal branches—contraction of bladder and of internal sphincter of anus.
- Stimulate central end of right hypogastric—contraction of bladder and of internal sphincter of anus.
- Stimulate right spinal branches —same effect.
- Stimulate ascending branches —doubtful effect.

¹ In these cases the peripheral end of the opposite hypogastric had less effect than usual on the internal sphincter; possibly section of the nerve on one side weakens the contractile power of the muscle.

Stimulate central end of right hypogastric —contraction of bladder and of internal sphincter.

Cut colonic branches and the left hypogastric.

Stimulate central end of right hypogastric —no effect.

Question of trophic centre in the inferior mesenteric ganglion.

If the trophic centre we are searching for, lay in the inferior mesenteric ganglion, section of all the nerves running from the spinal cord to the ganglion should leave the reflexes unaffected, supposing the change from afferent to efferent impulses to remain unaffected by the section. Four experiments (Series F) were made to decide this point. In three of these all the connections of the inferior mesenteric ganglion, except the mesenteric nerves and one hypogastric nerve, were severed; the other hypogastric being cut an inch or more from the ganglion, so that its central end could be stimulated later. Five days were allowed for the degeneration to proceed. In the fourth experiment, both hypogastrics were left intact, and on microscopic examination after death it was found that one small spinal branch running into the ganglion nearer the intestine than usual, had not been cut.

SERIES F.

Section of Spinal Branches of the Inferior Mesenteric Ganglion. (Cat.)

- No. 1. Branches to ganglion, and the right hypogastric cut 5 days previously. Give chloroform and A.C.E. mixture. Stimulate with weak tetanising currents.
Stimulate the central end of the right hypogastric—no effect upon the bladder, vas deferens, prostate vesicle, or internal sphincter of the anus.
The left hypogastric was tied and cut.
Stimulate the peripheral end of the left hypogastric—good contraction of the bladder, of the vas deferens and prostate vesicle, and slight contraction of the internal sphincter.
- No. 2. Branches to ganglion, and the left hypogastric nerve, cut 5 days previously. Give chloroform and A.C.E. mixture. Tetanising currents, weak to strong, tried.
Stimulation of the central end of the left hypogastric had no effect on the bladder, uterus or internal sphincter of the anus.
Stimulation of the central end of the colonic nerves gave no effect.
The right hypogastric was tied and cut.

Stimulation of the peripheral end of the right hypogastric gave good contraction of the bladder, slow but complete pallor of the uterus, and slight contraction, both circular and longitudinal, and slight to moderate contraction of the internal sphincter of the anus.

No. 3. Gave the same results in every point as No. 2.

No. 4. Branches to ganglia severed (save one small anterior branch) 14 days previously. Give ether and morphia, double tie and cut right hypogastric. Tetanising shocks of varying strengths from weak to strong employed.

Stimulation of central end of right hypogastric gave no trace of effect on the bladder; there was usually no trace of effect on the internal sphincter of the anus, but occasionally a slight contraction and pallor, which we could not definitely determine to be due to the rhythm.

Stimulation of the peripheral end of the right hypogastric gave good contraction of the bladder, good to moderate contraction of the internal sphincter of the anus, but rather more slowly than normal, and gradually complete pallor of the mucous membrane of the end of the rectum. The effect on the internal sphincter soon ceased if the stimuli were repeated at brief intervals. Stimulation of the peripheral end of the left hypogastric gave the same result.

The experiments in this series show that when the nerve-strands between the spinal cord and the inferior mesenteric ganglion are severed, and time allowed for degeneration, stimulation of the central end of one hypogastric does not produce the customary reflexes.

The absence of the reflex cannot, we think, be referred to a change in the nerve-cells of the ganglion, for the efferent fibres given off by the nerve-cells exert all their normal actions on the peripheral organs; they still are capable of causing contraction of the bladder, contraction of the internal sphincter of the anus, and so forth.

Hence, we conclude, that the nerve-fibres which carry impulses to the inferior mesenteric ganglion and set up the reflexes cannot have their trophic centre in that ganglion. The abolition of the reflexes in the circumstances mentioned above, puts out of court another possible explanation. A cell in the ganglion of one side might conceivably send efferent fibres down both hypogastric nerves. On stimulation of the central end of one of these fibres, an impulse must, so far as our knowledge goes, pass up to the cell, and it might be 'reflected' down the other branch of the cell proceeding to

the opposite hypogastric. Thus a reflex might be obtained involving efferent ganglionic nerve-fibres only. But since these fibres remain intact after section of the nerves to the ganglion, the reflex, if produced simply by efferent fibres from the ganglion, should persist; as it does not persist, we conclude that this passage down both hypogastric of fibres arising from one cell, whether it exists or not, will not account for the reflexes.

The possibility that motor fibres only are involved in the production of the reflexes is, nevertheless, not disproved by this experiment, for the passage of the stimulus from one nerve to another might be moved farther up the motor arc. This point will be more appropriately considered in the next section.

Question of trophic centre in the spinal cord or the spinal ganglia.

If the contention be accepted, that the trophic centre we are seeking is neither at the periphery nor in the inferior mesenteric ganglion, it can only be in ganglia of the posterior roots of the spinal nerves or in the spinal cord.

In the one case we may suppose that a fibre of a posterior root passes through the inferior mesenteric ganglion to its peripheral distribution, and on its way branches in such a manner that whatever other connections exist, a branch runs down one hypogastric and a branch runs to the opposite ganglion and makes connection physiologically with at least one nerve-cell there. On stimulating the central end of one hypogastric, the impulses would travel upwards towards the central nervous system, part—if we may use part in such relation—passing by the branch to the nerve-cell on the opposite side, and so giving rise to an efferent impulse passing down the opposite hypogastric.

A branch of this kind is now, after Golgi and Cajal, called a collateral. They and others have shown that the afferent fibres of the posterior roots give off collaterals to several segments of the spinal cord. The method of producing the reflexes which we are now considering, demands, that a collateral shall be given off by the afferent fibre outside the spinal cord; that on stimulating the nerve peripherally, impulses shall travel down the collateral; and that these impulses shall be able to set up other impulses in a sympathetic nerve-cell.

Clearly, the result might be produced by several different anatomical arrangements; the nerve might continue on in the hypogastric of the

same side and send its collateral to the ganglion of the opposite side, or pass to the hypogastric of the opposite side and send its collateral to the ganglion of the same side, and there are other possible arrangements unnecessary to mention.

In the other case, i.e. of the trophic centre being in the spinal cord, the fibres being fibres of the anterior roots, we have two courses open.

(a) We may make a similar set of suppositions to those required for the afferent fibres, and believe that the comparatively few motor fibres which are connected with cells peripherally of the inferior mesenteric ganglion¹ (cp. p. 420) are those which are concerned in bringing about the reflexes.

(b) We may take it that such fibres are insufficient in number, and that the motor fibre branches, one branch being connected with a cell on one side in the inferior mesenteric ganglion, the other branch being connected with a cell on the other. This view involves the assumption that an impulse can pass back through a cell into the motor fibre which runs to it, a view which does not seem a probable one, if, as Cajal's researches suggest, the motor fibre is not anatomically continuous with the cell, but ends near it in minute filaments.

We have already said (p. 423) that stimulation of the spinal nerves on one side causes impulses to pass down both hypogastrics. It is equally true that each hypogastric sends afferent fibres to the spinal nerves of both sides; this is easily seen by noting the reflex movements which occur on stimulating one hypogastric, after section of the spinal rami to the inferior mesenteric ganglion on the same or on the opposite side. Each hypogastric receives more efferent and more afferent fibres from its own side than it does from the opposite side of the spinal cord. The facts have to be borne in mind, but they do not help in deciding whether afferent or efferent fibres are the main elements of the reflex.

We have attempted to bring matters to an issue by cutting, in the spinal canal, the nerve-roots of those nerves which send fibres to the inferior mesenteric ganglion. The general result of investigation on the origin of the hypogastric fibres from the spinal cord, is that such fibres are given off in the IInd to the IVth or Vth lumbar nerves inclusive. Our own experiments had given us the same result as regards the great

¹ In this case we should obtain a reflex from any one of the branches of a nerve before it becomes connected with a nerve-cell, but should not expect to obtain it from the peripheral organs. Such reflexes can probably be produced in the spinal cord from fibres not usually classed as sensory fibres, e.g. those of the pyramidal tract.

majority of the fibres. Thus it appeared that it would be sufficient for our purpose if we severed the first five lumbar roots on both sides¹.

Section of the nerve-roots will of course bring in its train degeneration of the peripheral ends of all anterior root fibres; in the case of visceral fibres, this degeneration will extend to the nerve-cells with which the fibres are connected; the peripheral portions of the posterior root fibres will on the other hand remain intact. If, then, the roots of the first five lumbar nerves are cut, and time is left for degeneration, the inferior mesenteric ganglion and its branches, including both hypogastrics, will contain their normal contingent of afferent fibres, but should contain little, if any, of their normal contingent of efferent spinal fibres. Hence, if the reflexes are absent, there is *primâ facie* evidence that the normal reflexes are produced in motor fibres; if, on the other hand, they are still distinct, there is *primâ facie* evidence that the normal reflexes are produced in sensory fibres. There seemed then to be no difficulty in settling the question, and we were disagreeably surprised at obtaining diametrically opposite results in the first two experiments.

SERIES G.

*Section of the Roots of the Spinal Nerves*². (Cat.)

No. 1. Give ether. Cut 1 to v lumbar nerves inclusive on both sides between dura mater and ganglion of posterior root. One c.c. of morphia acetate injected subcutaneously. Next day cat purrs on being stroked, neither then nor later shows any sign of pain from the wound, which heals well.

Ten days later, ether again given. Double tie and cut right hypogastric about $\frac{3}{4}$ inch from inferior mesenteric ganglion. Tetanising current used, is felt distinctly, but not strongly, on the tip of the tongue.

Stimulate central end of hypogastric—no effect seen on bladder, there is some contraction of anus, viewed externally, but con-

¹ Section of the nerve-roots on one side is of course insufficient, since the nerve-roots of the opposite side supply both hypogastrics. We may mention, however, that owing to the kindness of Dr Sherrington we have made observations on two cats in which the first five lumbar roots were cut on one side only. The nerves had been cut by Dr Sherrington for the purpose of determining the sensory nerves of muscle, and we took the opportunity, when the animals were anæsthetized previously to being killed, of stimulating the central end of the hypogastric on the operated side. In both cases, the usual reflexes from the inferior mesenteric ganglion were produced.

² The operation causes more or less complete paralysis of the bladder. The bladder was emptied twice a day by compressing it through the abdominal walls.

traction is of external sphincter, and due apparently to a reflex from the exposed viscera. The least touch on the skin near the anus causes a vigorous contraction of the external sphincter.

Stimulate central end of hypogastric, the external sphincter being held open with forceps—no effect could be seen on the bladder, on the internal sphincter of the anus, or on the uterus. The stimulation was repeated many times; there was no effect except when the nerve was stimulated close to its ganglion.

Stimulate the peripheral end of the right hypogastric—good contraction of the bladder, moderate contraction of the internal sphincter of the anus, slow but complete pallor of the body of the uterus on the same side.

No. 2. The operation was the same as that of No. 1 except that one more nerve was cut on each side, viz. the viith lumbar.

Fourteen days later the animal was anaesthetized.

Stimulate the central end of the right hypogastric—decided contraction of the internal sphincter of the anus, and slight contraction of the bladder, chiefly near the ureter of the opposite side. The nerve was stimulated nearly an inch from the ganglion, and was well isolated.

Stimulate the obvious spinal branches successively—no effect.

Stimulate the ascending branch—contraction of the bladder and of the internal sphincter. (The nerve on microscopical examination was found to contain an undegenerated spinal branch.)

Stimulate the peripheral end of each hypogastric—normal effects. On dissection it was found that the 1st lumbar vertebra had a small rib attached to it, as there were 13 ribs above this, and only 6 lumbar vertebræ below, we call this the 1st lumbar vertebra and not the 14th thoracic. The lumbar and sacral nerves were of the posterior type.

We see that after degeneration of the motor fibres of the first five lumbar nerves, the reflexes in one case could not be observed, whilst in the other they were distinct. In the latter case it might be supposed that one of the spinal nerves was not completely severed; which would of course account for the persistence of the reflex. There cannot, however, be the least trace of doubt on this head; after section of the nerves, a curved instrument was placed under the upper end of the cord and so that it passed round the cord, projecting on both sides above the level of the spinal canal, this was drawn down to the lowermost level of the exposed cord. Moreover the dissection after the animal was killed

was quite decisive. We consider it perfectly certain that after degeneration of the motor fibres of the 1st to the 6th lumbar nerves inclusive, the hypogastric reflexes may still occur.

The debatable ground is so far narrowed that either the lower part of the thoracic spinal cord gives motor fibres to the hypogastrics, or the reflexes are produced by sensory spinal fibres of the lumbar nerves.

Having this in view, we made one other experiment, cutting the 11th and 12th thoracic nerves as well as the upper lumbar nerves. If after degeneration of the motor fibres in these nerves, the hypogastric reflexes were still obvious, we might fairly conclude that they were due to the stimulation of sensory fibres.

We give the abstract of this experiment.

No. 3. Ether given. The manner of conducting the operation was varied: the dura mater was cut open longitudinally, the cord cut through just above the nerve-roots of the 11th thoracic and removed down to the level of the upper part of the 5th lumbar vertebra; this involves severance of the roots of the 11th thoracic to the 6th lumbar inclusive, and probably of some roots of the lower lumbar nerves. The dura mater was left in the spinal canal. Next day the animal took milk readily and purred on being stroked. In a day or two there was some recovery of the anal reflex, this was the only reflex observed from the remaining lower portion of the spinal cord.

After six days, anæsthetics were again given, the right hypogastric was double tied and cut between the knots.

Stimulation of the central end of the hypogastric gave no effect on the bladder nor any obvious effect on the internal sphincter of the anus; this however was in a state of rhythmic contraction which made observation of slight effects difficult.

Stimulation of the peripheral end of the right hypogastric, and of the left uncut hypogastric, gave prompt and marked contraction both of bladder and internal sphincter.

Stimulation of the various spinal and of the ascending branches to the inferior mesenteric ganglion gave no obvious effect, but the observation of slight effects was interfered with by the spontaneous contraction of both bladder and sphincter.

Stimulation of the trunk of the sympathetic between the 5th and 6th lumbar ganglia gave no effect on the hairs of the tail, on the anus, penis or scrotum; it caused erection of hairs in a small patch on the back apparently in the region of the 5th and 4th lumbar ganglia.

Stimulation of the cut spinal nerves outside the dura mater, had no effect on the pelvic viscera.

Here as in experiment No. 1 no distinct reflexes could be obtained. Taking all the results into consideration we conclude that the reflexes involve motor fibres only. The reasons which weigh with us against the supposition that spinal sensory fibres are involved are,

a. The reflexes were absent in the two experiments No. 1 and No. 3, Series G, although the sensory fibres were intact. It is of course just possible this was due to individual variation, the ganglia or the peripheral structures being less responsive than usual; but this seems to us highly improbable, as we have never found the reflexes to be absent in the normal animal—the peripheral structures being directly observed as they were in these experiments.

b. Stimulation of the posterior roots of the lumbar nerves has no effect on the pelvic viscera. Similarly in Exp. 2 and 3 stimulation of the obvious spinal branches containing sensory but no motor fibres was without effect. If the normal reflexes were due to spinal sensory fibres, it would mean that stimulation of a sensory fibre peripherally of its collaterals gives rise to an effective impulse down the collateral, whilst stimulation of the fibre centrally of the collateral does not do so. This is inconsistent with the universally accepted view that a nervous impulse travels in a nerve-fibre equally well in either direction.

There is some proof of the presence of motor fibres from the lower thoracic nerves in Exp. No. 2. The obvious spinal branches to the ganglion were ineffective, whilst the ascending branch—the one which would be most likely to receive fibres from the thoracic nerves—gave peripheral effects, and was found on subsequent microscopical examination to contain an intact spinal branch.

For some time past we have made observations on the origin of the nerves which run to the pelvic viscera; we shall give an account of these in a later paper—we must confess that we have not so far obtained *decisive* effects on the bladder or internal sphincter of the anus by stimulating the XIIIth thoracic nerve, but we have sometimes observed slight effects which appeared to be due to the stimulation.

On the whole we think the balance of evidence is distinctly in favour of the view we put forward, viz. that the reflexes obtained on stimulating the central end of the hypogastric are due to nervous impulses which pass up motor fibres, and spread to the branches which they give off to the ganglia of the opposite side, and so down the opposite hypogastric nerve.

REFLEX ACTION OF THE GANGLIA OF THE SYMPATHETIC TRUNK.

The reflexes we have so far considered have been almost entirely reflexes from one side of the body to the other. In the thoracic and lumbar regions of the sympathetic trunk no connection exists between the ganglion of the two sides; so that in investigating these regions we can only obtain uncrossed reflexes. For some reflexes this fact is prejudicial to the investigation, for in cutting a nerve in order to stimulate its central end, we may cut the motor fibres to the region in which the reflex should be most manifest. But this does not apply in all cases. Thus if in the lower lumbar region there are fibres capable of producing a reflex in ganglia higher up, there should be no difficulty in determining their presence by observing the hairs which receive pilo-motor fibres from these ganglia.

No pilo-motor fibres issue from the spinal cord in the 5th lumbar or any lower lumbar nerve¹. If then the sympathetic be stimulated below the 5th lumbar ganglion, and this causes an erection of the hairs in regions supplied by ganglia above the point stimulated, the effect cannot be due to a stimulation of fibres which have joined the sympathetic below and are running upwards.

Now when the sympathetic trunk is cut just above the 7th lumbar ganglion, and the nerve is stimulated just above the cut, i.e. below the 6th lumbar ganglion, an erection of hairs takes place, as a rule, in the areas supplied by the 5th, 4th and 3rd lumbar ganglia, and sometimes in that supplied by the 2nd lumbar ganglion.

The number of hairs affected, and the extent of their movement is—broadly speaking—less, the higher the area.

This pilo-motor effect, as we have seen, cannot be due to ascending efferent pilo-motor fibres from the spinal cord. Nor is it due to fibres proceeding from the cells of the 7th lumbar ganglion; for the peripheral effect of such fibres would be uninfluenced by nicotin, whereas the fibres in question, by intra-vascular injection of 20 milligrams of nicotin, are rendered completely ineffective. Hence, the movement of the hairs takes place in consequence of nervous impulses passing centripetally along nerve-fibres and affecting nerve-cells. An action brought about in this way we may fairly speak of as a reflex action.

We give two experiments to illustrate the method employed, and to show some further results.

¹ Cp. Langley. *This Journal*, xv. 176. 1893.

SERIES H.

Pilo-Motor Reflex from Ganglia of Sympathetic Trunk.

In these experiments the hairs are cut short, and the region affected by each stimulation is marked by painting the upper and lower limits; towards the end of the experiment, the area supplied by each ganglion is determined. In order to make the account more easily intelligible we must assume that these areas are known at the beginning of an experiment. For brevity, the area of the skin supplied with pilo-motor fibres from the grey ramus of the 5th lumbar ganglion will be spoken of as the 5th area, and so with the others.

- No. 1. Cat. Chloroform. A.C.E. Cord removed from xiith thoracic downwards. Sympathetic exposed on the right side.
Tie sympathetic just above 7th lumbar ganglion, cut below ligature.
Stimulate below 6th L.G.—Strong movement of hairs in 5th area; rather weak and only near mid-line in 4th area; still weaker and nearer mid-line in 3rd area. With shocks not felt on tongue, the hairs move in 5th area only.
Tie and cut just above 6th lumbar ganglion.
Stimulate below 5th L.G.—Strong erection of hairs in 5th area, slightly less strong in 4th area, slight in median half of 3rd and 2nd areas.
Tie and cut just above 5th lumbar ganglion.
Stimulate below 4th L.G.—Moderate effect in 4th area, weak in 3rd and 2nd areas.
Stimulate below 5th L.G.—Hairs erect in 5th area only.
Tie and cut just above 4th lumbar ganglion.
Stimulate below 3rd L.G.—Moderate effect in 3rd, 2nd and 1st areas, most near mid-line, slight in parts of 13th thoracic area; requires rather strong stimulus.
Stimulate below 4th L.G.—Hairs erect in 4th area only.
Tie and cut below 3rd lumbar ganglion.
Stimulate below 2nd L.G.—Good in 2nd, 1st and 13th areas, and trace in 12th area.
Stimulate 1st lumbar spinal nerve in canal on left side.—Hairs erect in areas 1st lumbar to 2nd or 3rd sacral inclusive, very slight in last sacral area (over root of tail), strongest in 3rd, 4th, 5th lumbar areas.
- No. 2. The results of the part of this experiment which was conducted in the same manner as the preceding we may summarize thus

Part of Symp. stimulated.	Lumbar ganglia, areas of which were affected.
Below 7	7
Below 6	. 5 4 3
Below 5	5 4 3
Below 4	4 3
Below 3	3 2
Below 2	2 1

In areas, the number of which is in italics, the movement of the hairs was very slight. The grey ramus of the 6th lumbar ganglion, as usual, had no pilo-motor area.

20 milligrams of nicotin were then injected into the jugular.

Stimulate below 2nd lumbar ganglion — no effect.

„ ganglion itself	— hairs erect in 2nd area.
„ below 3rd L. G.	— no effect.
„ ganglion itself	— hairs erect in 3rd area.
„ below 4th L. G.	— hairs erect in 4th area ¹ .
„ ganglion itself	— „ „ „
„ below 5th L. G.	— no effect.
„ ganglion itself	— hairs erect in 5th area.
„ below 6th L. G.	— no effect.
„ ganglion itself	— no effect.
„ below 7th L. G.	— no effect.
„ ganglion itself	— hairs erect in 7th area.

It will be noticed in these two experiments that the number of ganglia brought into action by stimulating a given point of the sympathetic is not always the same. We have found other variations, either more or fewer ganglia being involved, but the consideration of these variations is unnecessary for our present purpose. It is perhaps worth while to point out that in an accurate determination of the ganglia involved, the white rami communicantes must be cut, since these, in the lumbar region, commonly carry some fibres from one ganglion to the area of the immediately anterior ganglion. We have not found that the presence of the spinal cord influences the results, except in so far as a reflex movement of the body will probably occur on stimulating the sympathetic.

Above we have shown those actions to be reflex actions, which occur on stimulating the anterior end of the sympathetic, in the region where the sympathetic receives no pilo-motor fibres from the adjacent spinal nerves. The lumbar sympathetic from the 1st to the 5th or 6th lumbar

¹ The effect was absent in the other similar experiments.

ganglia does receive pilo-motor fibres from the adjoining nerves, but since all these fibres descend the sympathetic, the argument used above is applicable also to show that reflex actions are obtained from the upper lumbar sympathetic. They cannot be due to stimulation of fibres arising from the cord lower down and ascending the sympathetic, and they are abolished by nicotin.

We conclude then that on stimulating any point of the lumbar sympathetic a reflex action is produced involving two to four of the ganglia immediately anterior to the point stimulated.

We cannot at present give decisive evidence as to the way in which these reflexes are produced, but we are inclined to believe that each efferent spinal fibre of the sympathetic trunk sends branches and supplies several (approximately four) sympathetic ganglia, and that stimulation of the fibre in any part of its course will cause an impulse to pass to each of the ganglia with which it is connected. In fact, we think that these reflexes, like the hypogastric reflexes, involve motor fibres only.

We have evidence of other similar actions, but the account of these we defer, until we are able to give a more conclusive statement as to the method of production of the pilo-motor reflexes.

SUMMARY.

There is as yet no satisfactory evidence to disprove the view that the secretion of saliva obtained on stimulating the central end of the lingual after section of the chordo-lingual nerve is due to recurrent chorda tympani fibres.

We confirm, in a number of ways, the account given by Sokownin and others, viz. that after section of the nervous connections of the inferior mesenteric ganglion, other than the hypogastric nerves, a contraction of the bladder is obtained by stimulating the central end of one hypogastric, the efferent impulses passing down the opposite hypogastric.

This action is not due to recurrent fibres from the sacral nerves, for after the nerves to one side of the bladder are cut, stimulation on the same side, of the sacral nerves in the spinal canal or of the nervus erigens does not cause contraction. Nor is it due to recurrent fibres from the lumbar nerves. For after cutting the spinal branches of the inferior mesenteric ganglion and cutting on one side the nerves to the

bladder, stimulation of the lumbar nerves on that side has no effect on the bladder.

Stimulation of the central end of one hypogastric causes, in addition to contraction of the bladder, contraction of the internal sphincter of the anus, pallor of the mucous membrane of the rectum, slight pallor of the cornu and body of the uterus on the opposite side (or of the vas deferens and prostate vesicle), and, rarely, slight contraction of the opposite cornu of the uterus, and of the vagina. All of these actions are temporarily annulled by injecting 10 to 20 milligrams of nicotin into a vein; in this case the impulses set up in the central end of the hypogastric are blocked in the inferior mesenteric ganglion, for nicotin does not annul the effects of stimulating the peripheral ends of the hypogastrics.

Thus the impulses passing up one hypogastric, traverse nerve-cells in the inferior mesenteric ganglion, before they can reach the opposite hypogastric. We may then properly call the various actions we have described, reflex actions. In the further inquiry we assume that the nerve-fibres have one trophic centre—a nerve-cell—and one only. When one hypogastric nerve is cut, and time left for degeneration of nerve-fibres, the reflexes can still be obtained from the central end of the nerve, so that reflexes cannot be due to fibres proceeding from nerve-cells on the peripheral course of the hypogastrics.

When the spinal branches to the inferior mesenteric ganglion are cut, and time left for degeneration, the central end of the hypogastric gives no reflexes, the peripheral ends of the hypogastric give their customary effects; thus the normal reflexes cannot be due to nerve-cells in the ganglion sending out two sets of fibres, one passing down one hypogastric, and the other down the other hypogastric; further, the nerve-fibres in the central end of the hypogastric which subserve the reflexes must have their trophic centre, i.e. be connected with nerve cells, either in the ganglion of the posterior root or in the spinal cord.

When the 1st to the 7th lumbar nerves on both sides are cut centrally of the posterior root ganglion, and time is left for degeneration, the hypogastric reflexes may be abolished or may persist. We are inclined to think that the persistence, when it occurs, is due to some motor fibres running from the lower thoracic spinal nerves to the inferior mesenteric ganglion, and accordingly that the reflexes are due to the stimulation in the hypogastric of the central ends of motor fibres, which in the inferior mesenteric ganglion give a branch to the nerve-cells of the opposite hypogastric.

Reflexes can also be obtained from the trunk of the sympathetic. When any part of the lumbar sympathetic chain is stimulated, erection of hairs occurs in the areas supplied by two to four ganglia above the point stimulated. This is not due to fibres coming from the spinal cord and ascending in the sympathetic, for in the lumbar region there are no such ascending fibres. It is not due to fibres proceeding from ganglia below the point stimulated, for nicotin abolishes the action, and does not abolish the pilo-motor action of the grey rami of the ganglia. We think it probable that the reflexes are due to the stimulation of spinal motor fibres connected with several ganglia, the impulses ascending the fibres and passing to their several branches. But on this point, as on the corresponding point in connection with the hypogastric reflexes, we think further experiments desirable.

For convenience we have spoken of the various actions we have described as reflexes. If our tentative view, that they are produced by motor nerves, is correct, it is clear that the term reflex is used in an unusual sense. For the present, we prefer straining the nomenclature to introducing a new term.